

Constancy to horticultural varieties shown by butterflies, and its possible evolutionary significance

BY

KRISHNA RAO DRONAMRAJU AND HELEN SPURWAY

Indian Statistical Institute, Calcutta-35

Since Aristotle it has been known that bees of a particular colony showed a constancy to one species of flower until the local population of this was exhausted of its nectar. Recent discussions (e.g. Ribbands 1953, Butler 1954) are agreed that a few workers of a hive scout for adequate sources, and inform their comrades, who exploit these sources to exhaustion before turning their attention to newly discovered supplies. Mather (1947) has shown that in the genus *Antirrhinum* at least, this constancy is species specific.

While working in a small experimental garden consisting of three plants each of two colour varieties of the primarily South American species *Lantana camara* L. Dronamraju (1958) observed that the different varieties were preferentially visited by different species of butterflies. The two varieties of *Lantana* are those which are overwhelmingly preponderant among the feral population around Calcutta. In one called *pink* the newly opened florets are white except for the yellow honey guides, but the unopened buds and the ageing florets at the periphery of the inflorescence are pink. In the other variety called *orange* the buds and ageing florets are orange and the young florets yellow. Both forms set seed, and the specimens in our garden were collected as seedlings. It has so far proved impossible to cross these two varieties, and Dr. E. K. Janaki Ammal tells us that it is probable that they are of different ploidies. K.R.D. began watching the garden again next spring and has now spent 46.75 hours all told attempting to note all visits of all species of insects. Among these were 9 species of Papilionoidea. We have also casually observed other species of butterflies at other times and seasons, in other places, on the same varieties, and on other varieties, (and perhaps species), of *Lantana*.

Table 1 shows the data collected for the six most frequent visitors (Dronamraju 1960). The unit counted is the insertion of the proboscis into a floret, from now on to be called a *feed*. The movements of

TABLE 1

Species	Family	Date of		Number of days observed	Number of feeds	
		1st observation	last observation		on orange	on pink
<i>Precis almana</i>	Nymphalidae	29-5-58	21-4-59	16	218	13
<i>Danais chrysippus</i>	Danaidae	19-3-59	22-5-59	18	142	152
<i>Papilio polytes</i>	Papilionidae	19-3-59	4-4-59	4	15	31
<i>Papilio demoleus</i>	Papilionidae	19-3-59	19-5-59	13	42	98
<i>Catopsilia pyranthe</i>	Pieridae	29-5-58	22-5-59	27	40	603
<i>Baoris mathias</i>	Hesperiidae	19-3-59	19-5-59	12	1	108

normally feeding butterflies are sufficiently slow for these feeds to be counted. Only in the counts of *Baoris mathias* is it believed that the movements were so rapid that any large number of feeds were unnoted. Such an underestimate would increase the significance of the preference for pink shown by this butterfly. Smaller data on other species showed statistically significant preferences, but because they were collected during too short a period of time they may only record individual preferences, or temporary constancies such as are known for *Apis mellifera*, and were observed during this same series of observations for *A. florea*.

On the totals it is clear that 5 species have a distinct preference for one colour variety rather than the other. The length of the periods during which the observations were made, and in some species the use of individuals which were sexually dimorphic, or marked by injury, or paint, makes it clear that several individuals of each species were observed. We cannot assume that all these individuals either had indistinguishable experiences, or alternatively were influenced by some previously unsuspected social reaction to a variety first visited by one individual. Therefore we think that these data make it most unlikely that an individual butterfly of these species emerges from its pupa indifferent to which colour of *Lantana* it feeds upon, and becomes conditioned or imprinted by its own individual experience.

Danais chrysippus judged by the totals given in Table 1 has no preference. However the data are highly heterogeneous. Statistical estimation cannot be made because so many observation periods included only one or two feeds.

Therefore we give (Table 2) the number of feeds during the two hours when most visits of this species were recorded. Both were between 8 and 9 a.m.

TABLE 2

Date	Orange	Pink
22-3-59	0	46
7-5-59	50	7

Formally such counts resemble those that are obtained by watching a colony of bees visiting a mixed crop, but before we postulate that *Danais chrysippus* has a social organisation, we will discuss our observations on the first feeding behaviour of twelve individuals of *Papilio demoleus* that emerged from their pupae in the laboratory.

This species is the only one of those observed of which we have obtained larvae to experiment upon. Professor B. Rensch in a letter

to Professor J. B. S. Haldane commenting on Dronamraju's paper of 1958 had suggested that these preferences might be due to the butterflies becoming imprinted to flowers of the colour of their first feed. Therefore, because wild *P. demoleus* showed a significant but not extreme preference for pink, we exposed ten of these twelve animals to orange flowers alone, including holding them on to the inflorescences if they did not alight voluntarily. After at least half an hour if they did not feed, or after at least 40 feeds if they accepted orange, pink was presented. The other two butterflies were offered a choice. One (σ 4) always flew away when held on inflorescences of either colour during the hour's observation period, though he inserted his proboscis once into an inflorescence. This was a pink inflorescence on which he had been placed and on which he subsequently remained unfeeding for 17 minutes, only leaving when disturbed. Next day he was not offered a choice and refused orange for half an hour but then accepted pink. The record of the other animal offered a choice (σ 7) is graphed in Fig. 2.

Any number from 4 to 40 inflorescences of one colour were offered on cut stems, and care was taken to match the specimens of the two colours in number and condition to human eyes. Also note was taken as to whether the flowers were freshly gathered, previously used that day for butterfly feeding experiments, or the present mature flower's had opened in the laboratory sheltered from any insect visits. We have only tenuous evidence that our flowers were ever exhausted enough for their interest to decrease for a butterfly.

At first the experiments were performed in a large room with windows in three walls. One butterfly fed on orange and was immediately eaten by a gecko; another refused orange for 2 hours and 40 minutes and then walked through a draining hole—and instead of flying away fell from four storeys and was recovered (she was marked) with a fractured costa! The third produced clear results and was observed on 6 consecutive days. All other animals were observed in a small wire and wood cage $2.1 \times 1.5 \times 2$ cu. m. in volume. Two people were necessary, one to observe (usually KRD) and one to write (usually HS), mainly but not exclusively from dictation, because the butterflies, being starved, fed more rapidly than free animals. No sugar water had been given before the experiments to be described.

Table 3 sums up our conclusions, and Figs. 1 and 2 graph two experiments to demonstrate the behaviour which we categorise as 'feeds on orange; prefers pink'. In both the figures the horizontal axis represents time, and there are four distinct vertical axes. The black

TABLE 3

Papilio demoleus
First feeds in captivity

	Prefers Orange	Prefers Pink	?
Feeds on Orange ..	3	3	1
Does NOT feed on Orange	4	1

histograms represent separately the number of feeds on orange and pink, and the white histograms the number of landings, i.e. the number

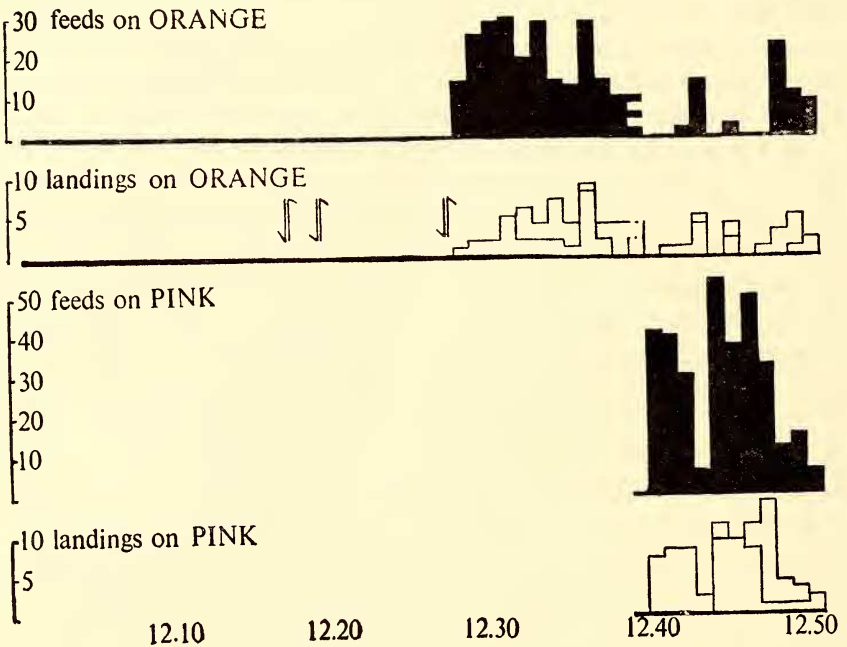


Fig. 1.

Papilio demoleus ♀3 feeding on *Lantana camara* 24-8-1959.

of times the butterfly alighted and stood on an inflorescence. We have never seen a *Papilio demoleus* feed without landing, but these butterflies often land without feeding. The horizontal lines represent the period of time when flowers of that colour were present. Pink was

only presented to ♀ 3 (Fig. 1) at 12.39 hours, after the animal had fed upon orange; pink was removed from ♂ 7 (Fig. 2) at 16.14 hours, after it had been fed upon, and returned at 16.24; orange was present throughout both experiments. In the experiment with ♀ 3 two vases of both colours were presented and the histograms of landings are divided into two parts to indicate when she flew from one vase to another. When all four vases were presented they were arranged alternately in a row so that a vase of another colour had to be flown over with every change. In Fig. 1 the arrows indicate when the animal

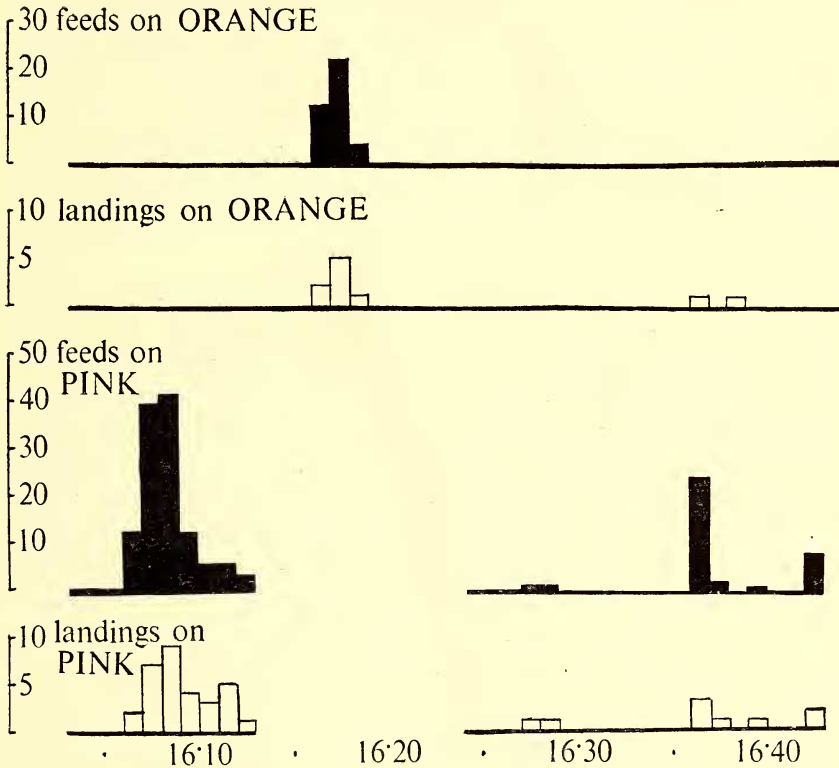


Fig. 2.

Papilio demoleus ♂7 feeding on *Lantana camara* 28-8-1959.

was forcibly held on to the flowers. She always flew away when released. The dotted histograms represent feeds and landings uncounted because the observers were occupied in introducing the vases of pink flowers. It will be seen that both these animals did feed on orange, but were reluctant to do so especially in the presence of pink. The second supply of pink offered to ♂ 7 consisted of only

four inflorescences which had been ardently fed upon (194 feeds) five hours before. Nevertheless they held his attention from the four orange to which he only had had access, and on which he had only fed 36 times.

The series of experiments summarised in table 3 support the theory that most individuals of *P. demoleus* emerge from their pupa with a preference for feeding on pink *Lantana* rather than orange and that this is not altered by receiving their first food from orange flowers. The three animals who continued to feed on orange after pink was made available were a mother, one son, and one daughter. The father and another son and daughter were tested and preferred pink. Thus a minority of *P. demoleus* prefer orange in the sense of behaving thus in our experimental conditions. If this difference is genetically determined it is a behavioural polymorphism, and a similar polymorphism present in *Danaïd chrysippus* would explain the observations on wild animals in Table 2. A similar heterogeneity can be discerned in the data on wild *P. demoleus*, but the individual observations are too few for this to be demonstrated as significant.

We have been able to find only one previous recording of a similar phenomenon. Eltringham (1933) observed specimens of *Vanessa urticae* (an orange Nymphalid not unlike *Precis almana*) visiting a bed of asters (Compositae) of which white, purple, and pink flowers were in the approximate proportions 7:9:12. However, out of 427 visits 47 were to white, 245 were to purple, and only 135 were to pink (from discussion by Ford 1945 who gives more details). These observations raised the question of whether the animals distinguished by colour vision, and led to the establishment of the fact of colour vision in butterflies (discussed by Ford *loc. cit.*). However its relevance to these flower preferences was not established, and the same question must be asked about our own observations. Because a pink-preferring butterfly does in our experiments feed on pink, white, and heliotrope flowers of other nectar-bearing species, while ignoring nectar-bearing orange and yellow flowers, we believe that these animals are reacting to colour and not to some other stimuli correlated with it in these *Lantana* stocks. However we do not want to stress this belief yet, as the flowers presented were very heterogeneous in structure, and not every species with pink flowers was visited.

Whatever the nature of the stimulus, such preferences will exert a selection pressure on the plant population comparable to that exerted by sexual selection in animals. A learnt preference will exert much less selection; a bee changes its behaviour to accommodate, or to adapt to, every change in the source of nectar. An instinctive preference

will either sterilize a new mutant because few or no pollinators visit it; or preserve the phenotype because it is pollinated by animals who rarely mix its pollen with that of the unchanged parental population, i.e. whose behaviour favours homogamy. So if a new mutant is recessive the butterflies' behaviour will maintain homozygosity once a few homozygotes have segregated in a population; if the mutant is a dominant so that the first unusual phenotype is a heterozygote this will be self-pollinated by the pollinators and so produce homozygotes which will be maintained by the same behaviour. The two phenotypes will be more or less isolated sexually, and thus have the possibility to become further differentiated. In short is this an insect capacity which could make possible in a plant population the initiation of sympatric speciation by a single gene mutation? Mayr (1947) considered and rejected the possibility of sexual isolation arising by a mutation producing a change in a preference. The butterflies we have described have established preferences and it is these which could exercise selection pressure on any mutants that altered relevant stimuli.

REFERENCES

- Butler, C. G. (1954): The world of the honey bee. London. Collins.
- Dronamraju, K. R. (1958): The visits of insects to different coloured flowers of *Lantana camara* L. *Curr. Sci.* 27: 452-453.
- — — (1960): Selective visits of butterflies to flowers, a possible factor in sympatric speciation. *Nature*, Lond. 186: 178.
- Eltringham, H. (1933): The senses of insects. London, Methuen.
- Ford, E. B. (1945): Butterflies. London. Collins.
- Mather, K. (1947): Species crosses in *Antirrhinum* I. Genetic isolation of the species *majus*, *glutinosum*, and *orantium*. *Heredity* 1: 175-186.
- Mayr, E. (1947): Ecological factors in speciation. *Evolution* 1: 263-283.
- Ribbands, C. R. (1953): The behaviour and social life of honey bees. London. Bee Research Association Limited.